THE LIFE HISTORY AND BIOLOGY OF A MARINE HARPACTICOID COPEPOD, TISBE FURCATA (BAIRD)[1]

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Introduction

Only a few free-living marine copepods have been reared with a view to determining the details of their complete life histories. This can no doubt be attributed to the difficulty experienced in culturing most species through the entire life cycle. Considerable literature has accumulated on the morphology of developmental stages and on certain aspects of the biology, particularly of the more important planktonic calanoid species, especially *Calanus finmarchicus*. This species has also been reared through its entire life cycle in cultures (Lebour, 1916), and its biology studied under laboratory conditions more recently by Raymont and Gross (1942). The cyclopoid, *Oithonina nana,* has also been reared through the developmental stages (Murphy, 1923). But pertinent questions relative to the age at maturity, fecundity, and life span of individuals have received scant attention for other marine species. The fresh-water copepods on the other hand have been the subject of a large amount of investigation and much detail is known about their life histories and reproduction (see especially Gurney, 1931; Ewers, 1930, 1936).

Of the marine harpacticoids, *Longipedia coronata* Claus, *L. scotti* G. O. Sars, and *L. minor* T. A. Scott have been reared sufficiently to reveal specially significant aspects of their biology (A. G. Nicholls, 1935). *Tigriopus fulvus* (Fischer) has also been studied in considerable detail by Fraser (1936) and Shaw (1938). The morphology of the larval stages of a number of other marine harpacticoids has been described by various investigators, especially Chappuis (1916), Brian (1919, 1922), Gurney (1930, 1932), and Nicholls (1941). Many of the littoral species, though less conspicuous than planktonic copepods, fill an important niche as microscavengers on the bottom, and therefore warrant a close study for ecological reasons.

Tisbe furcata, also known under the generic names of *Idya* and *Idyae* (see Wilson, 1932), is a littoral cosmopolitan species. It thrives in cultures and therefore often occurs as a contaminant in laboratory cultures of other organisms. At Scripps Institution it is constantly present in the salt-water system, aquariums, etc., to which it gains entrance from the sea through the pumping system.

In 1934 it occurred in such numbers that it contributed materially to formation of flocculent detritus in the pipes. This detritus when matted together with loosened calcareous tubes of *Spirorbis* (also established in the system) caused serious clogging of water delivery jets in the aquariums.

There is some possibility that "culture forms," characterized by small differences in proportions of appendage segments and strength of setae, may develop in *Tisbe* in these cases of isolation or semi-isolation from the "wild" population. However,

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Monk (1941) considers the present form to be a new variety, *johnsoni*. Controlled tests were not made of the factors involved in development of culture forms, but the temperature range (about 17–21° C.) over which the animals were reared is small compared to that used by Coker (1934) in experiments affecting the form of fresh-water *Cyclops*.

In nature *Tisbe furcata* is usually found in shallow water among algae or on the bottom where it is frequently the dominant species, but being capable of swimming, it is sometimes found also in the coastal plankton. Sars (1903–1911), who has given a full description of the adult, found it to be the most widespread of the harpacticoids in Norway wherefrom he also reports a large deep-water form of the species.

The Developmental Stages

During its life cycle *Tisbe furcata* passes through six naupliar and six copepodid stages, the last of which is the adult. The female is about 1.0 mm. and male 0.7 mm. long. The instars are separated by only one molt as in other copepods that have been studied. The female carries the eggs in a single egg-sac attached to the genital segment. The early cleavage and embryological stages have been studied by Witschi (1934).

All drawings have been made from specimens reared in the culture experiments to be described later. The assistance of Dr. Cecil R. Monk is gratefully acknowledged in connection with the 1938 cultures and with the developmental stages.

Naupliar Stages

(Plate I, Figs. 1 to 6)

In all these stages the larvae are normally benthonic, but occasionally they are taken in the plankton near shore where they have been swept off the bottom by water currents. They are colorless, subcircular in outline and possess a small red eye spot.

Nauplius Stage I (Fig. 1).—Average length 0.062 mm.; labrum circular flap; first antennae three-segmented, the distal segment with three terminal setae; the second antennae strongly built, the endopod terminating in a prehensile hook, exopod normal. The first basis of the second antennae is provided with a large but rudimentary masticatory blade or hook with a small seta at its base, and the second basis bears two strong spines. The mandibular palp possesses a splender exopod of three indistinct segments, the distal segment bearing one short and one very long seta; the endopod bears two strong short hooks and two setae. The caudal armature consists of two rather long flaccid setae.

Nauplius Stage II (Fig. 2).—Average length 0.082 mm. The obvious structural advancements over Stage I consist of increase in strength of the masticatory blade of the second antennae and the appearance of two strong setae, one each on either side of the posterior ventral side. These setae are the earliest visible fundaments of the first maxillae. This early appearance of the maxillae is characteristic of the harpacticoids. In the strange nauplius larvae of *Longipedia* the first maxillae are present already in the first stage (Nicholls, 1935). In this respect the development of harpacticoids is similar to that of many cyclopoids. In calanoids the rudiments of these appendages first appear in the third or fourth nauplius stage.

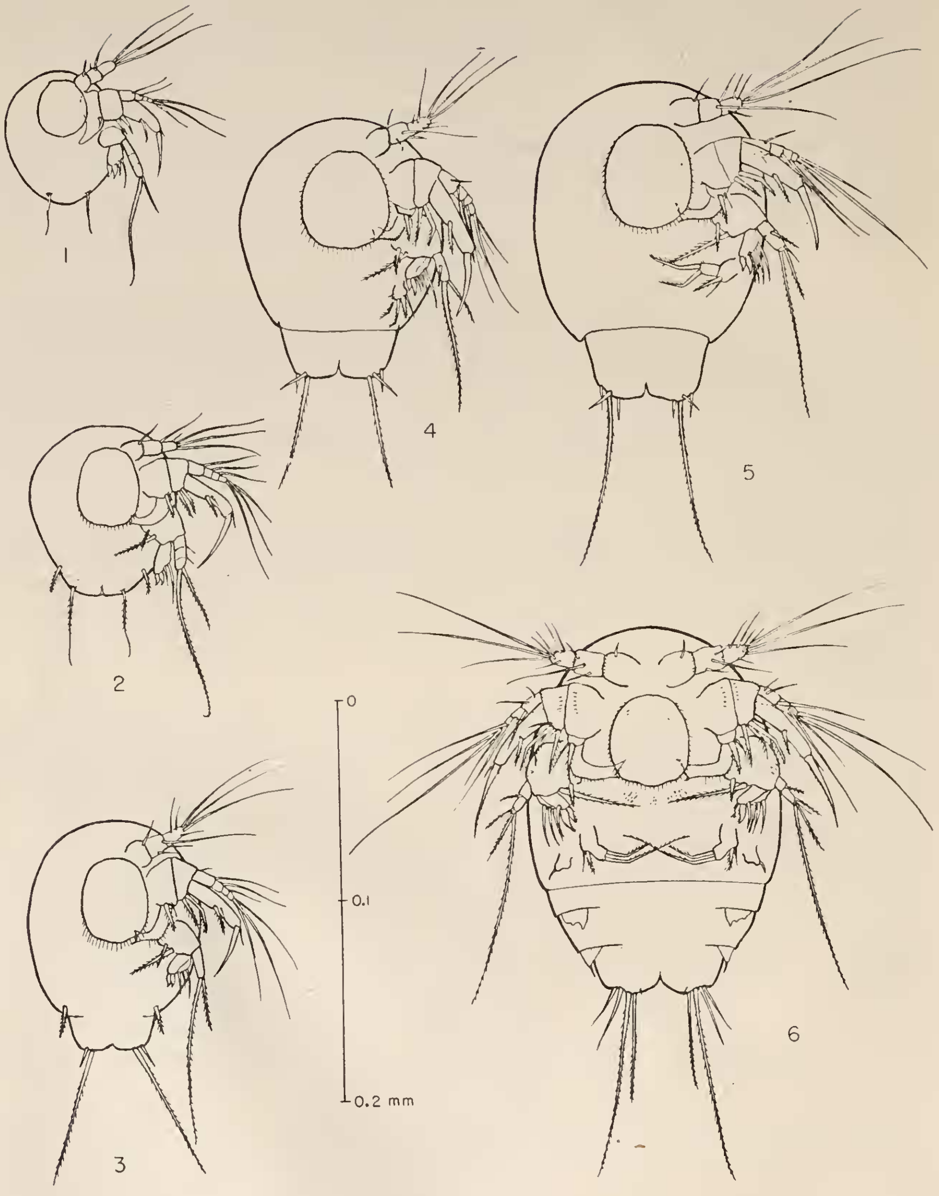

PLATE I

Development of *Tisbe furcata*

FIGURES 1–6. Nauplius stages I to VI—ventral; all drawn to same scale with aid of camera lucida.

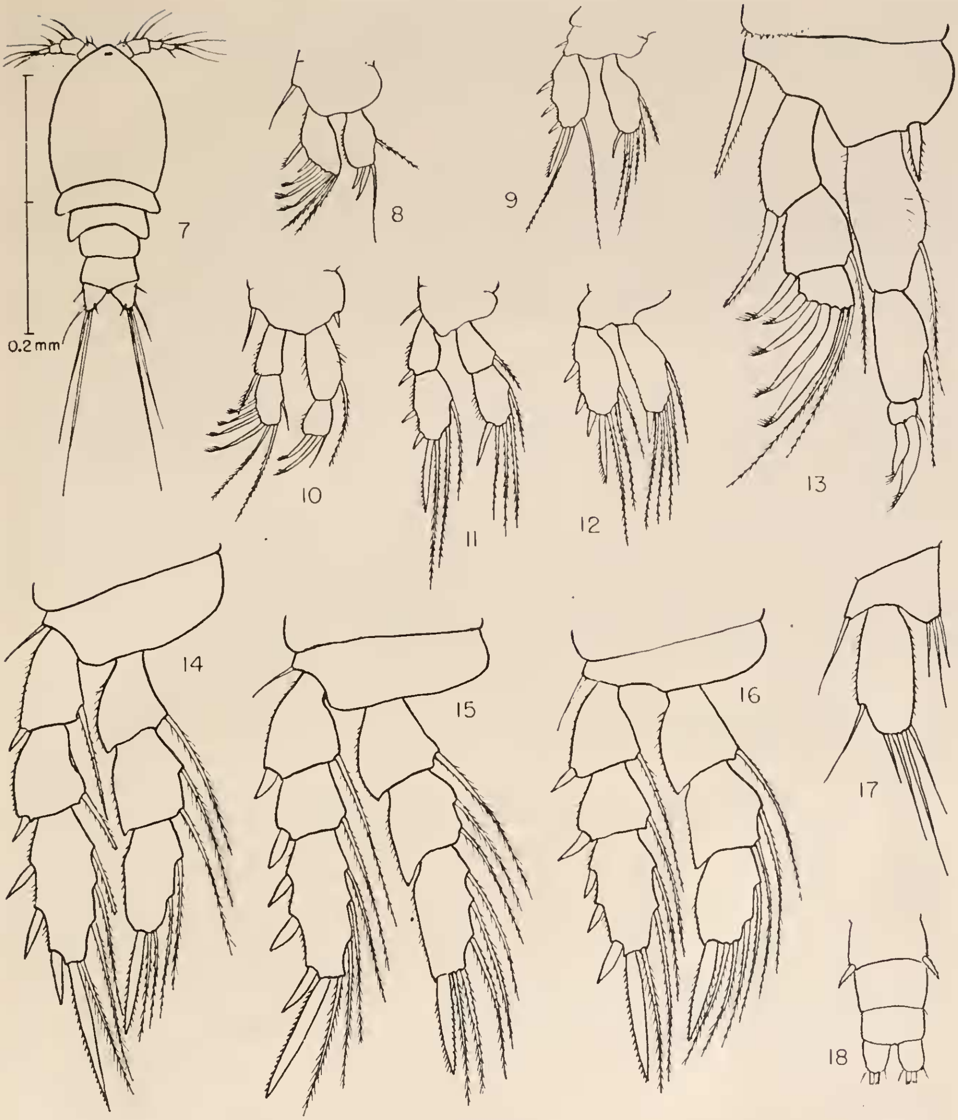

PLATE II

Development of *Tisbe furcata*

(*Camera lucida* drawings)

FIGURE 7. Copepodid stage I—dorsal.

FIGURES 8 and 9. First and second feet—Copepodid stage I.

FIGURES 10, 11, AND 12. First, second and third feet—Copepodid stage II.

FIGURES 13, 14, 15, 16, AND 17. First, second, third, fourth, and fifth feet—Copepodid stage V—female.

FIGURE 18. Posterior ventral portion of urosome of male copepodid stage IV to show sixth feet as represented by spines.

Nauplius Stage III (Fig. 3).—Average length 0.110 mm. As in II, but with three marginal setae on the distal segment of the first antennae, one additional seta on the endopod of the mandibular palp, and one short seta issuing from the outer angle of each caudal ramus. The original caudal setae are now much longer and more rigid than before.

Nauplius Stage IV (Fig. 4).—Average length 0.130 mm. As in III, but posterior segment of body more clearly defined. The distal segment of first antennae with increased number of marginal setae that can be discerned only with difficulty and are therefore not useful in identification as in calanoid larvae. The endopod of mandibular palp with four setae; the first maxillae, each showing one segment with three spines and a long seta; each caudal ramus with two short outer setae at the base of the long seta.

Nauplius Stage V (Fig. 5).—Average length 0.156 mm. As in IV, but the rudimentary first maxillae have two segments each, the distal segment with two strong curved spines and the proximal with one spine and one seta. Caudal ramus each with an additional short seta set at the inner base of the long seta making a total of three short setae.

Nauplius Stage VI (Fig. 6).—Average length 0.178 mm. As in V, but distal segment of first antenna with five marginal setae; one-segmented rudiment of second maxilla is evident with one short seta; rudiments of first and second pairs of legs present but the maxillipeds were not evident. Caudal armature as in V, but the formerly short setae are much longer, especially the inner pair.

Copepodid Stages

(Plate II, Figs. 7 to 18)

The sixth nauplius stage metamorphoses to the first of six copepodid stages, the last of which is the adult. The period required to pass from hatching of the first nauplius to the last copepodid is about 16 days at temperatures of 17° to 21° C.

The first copepodid stage is 0.20 mm. long and resembles the adult in general appearance, but there are present only the first two pairs of feet with a rudiment of the third pair and the metasome and urosome have respectively only three and two divisions, using the terminology of Sars. In subsequent stages one additional pair of feet is added for each molt except the fifth.

The order of segmentation of the feet follows the same pattern as that found in calanoid copepods. Each pair of feet at the time of its appearance possesses only one segment in each ramus, and in the next following molt each ramus becomes two-segmented and remains thus until the fifth molt (Copepodid V) when the rami of all the feet, 1 to 4, acquire three segments each (Plate II, Figs. 13–16). The new segment is derived from the proximal portion of the distal segment. This is illustrated in the first pair of feet which already in the fifth copepodid stage furnish diagnostic features of the genus. The fifth pair of feet which furnish the specific characters are not completely diagnostic until the sixth copepodid stage.

The sexes are readily separable morphologically in the fourth copepodid stage. The male in this stage is not only smaller in body size but the sixth pair of feet is already clearly developed, each foot represented by a small spine (Plate II, Fig. 18).

In the female these feet are wanting or indistinguishable from the row of fine spines on the urosome.

The Biology of Tisbe Furcata

Culture experiments

Syracuse watch glasses and low stender dishes of 50 ml. capacity were used for culture dishes in order to facilitate direct examination under the low-power microscope. The water used in the dishes was filtered to eliminate the possibility of contamination with foreign eggs or nauplii from the general sea-water supply. A fairly constant temperature was maintained by keeping the culture dishes on a table of running sea water, though the animals thrive in dishes kept at ordinary room temperatures.

A variety of marine foods was tested including ground dried mussels and scallops, dehydrated kelp, fresh seaweed and fecal pellets of *Nereis*. Each of these given individually in very small amounts was quite satisfactory as food. Shavings of fresh brown seaweed or dehydrated kelp appeared to be the best single food. Fresh seaweed has the disadvantage that the slime secreted tends to entrap the organisms. In general, however, the cultures were fed various mixtures of the above items so that some measure of selection was possible for the animals. About twice a week the dishes were cleaned by removing the debris and about one half of the water with a pipette, and a fresh supply of water and food added.

Life history series were obtained in four separate years, i.e., March-May 1935, June-July 1938, April-June 1942, and Sept.-Dec. 1947. During this time 30 or more broods and some of their progeny for two generations were studied more or less completely. During these periods no marked seasonal changes were observed in the breeding habits, or rate of reproduction, though a somewhat higher average number of eggs per egg-sac was noted in December.

Since observations on the 1942 series were the most continuous, they will form the main basis for discussing the salient features in the biology and life cycle of this species. Where data can be drawn from the earlier or later cultures, they will be made a part of the summary of time involved in the various phases or periods of the life cycle.

The lapse of time given for the various periods is the minimum time, or the average of several observed minima. For example, the first appearance of a nauplius in a culture was set as the beginning of the naupliar period and the first appearance of a copepodid marked the end of the naupliar period for any one brood.

Number of eggs produced

In order to obtain an estimate of the average number of eggs produced by each female per brood, counts were made of the eggs in the brood sacs of ten ovigerous females selected at random from the general population in March 1942. The number ranged from 29 to 82, with an average of 42.9 eggs per sac. There is obviously a very wide range in the number of eggs produced per egg-sac depending upon how long the individual has been laying eggs, and perhaps also upon the season. A check count was made in December 1947 in which the numbers ranged from 45 to 93 with an average of 72 eggs in each of 12 egg-sacs. Kunz (1935) reports 30 to 41 eggs for the species in Kiel Bay.

A group of ten ovigerous females was selected at random from the same population from which the 1942 egg counts were made and isolated for experimental culture, two females per dish. Each female was removed from the dish as soon as her eggs had all hatched. Thus each of the five culture dishes contained the nauplii from two egg-sacs. Careful account was kept of each population. As they matured and the adults mated, each mating pair was removed, recorded, and placed in another dish. In this way an accurate census was obtained.

Success of hatching and survival

From the ten broods 343 individual animals reached maturity. This indicates about 80 per cent survival, if we assume that the average egg-sac contains 43 eggs.

Incubation period

The duration of the incubation period was approximated by noting the first appearance of the egg-sac and the subsequent hatching of the nauplius larvae from the sac. The minima obtained ranged from two to four days. On the basis of the average of 21 cases the period was 2.5 days. Usually the cultures were examined every one to three days.

Naupliar period

The time required for completion of the separate stages was not studied. During the naupliar stages the animals creep about actively over the bottom or cling to detritus, etc., by means of prehensile hooks on the second antennae (Plate I, Figs. 1–6). The duration of this period is from three to eight days, with an average minimum of five days based on 22 brood histories.

Sex ratios

Of the 343 individuals reaching maturity 114 or only 33.3 per cent were females. One culture dish produced 34 females and 33 males, but in all of the rest the males were in great majority. In order to compare this unequal sex ratio in the culture dishes with that of the general population an examination was made of 44 adults from the water system. Of these only 41 per cent were females. Additional analysis involving 98 specimens reared in December 1947 also showed a ratio of one female to two males.

The numerical dominance of males is of considerable interest since usually in other species of copepods the females are the more numerous, sometimes overwhelmingly so. This inequality of the sexes is often seasonal, but no seasonality has come to light in the study of *Tisbe*.

In a study of the tide pool harpacticoid *Tigriopus fulvus,* Tsen-Hwang Shaw (1938) found 58.8 per cent females in a collection of 318 specimens.

Sexual maturity

A study of the rate at which sexual maturity was attained by 87 pairs of the 343 individuals hatched from the ten egg-sacs mentioned above, showed that two pairs began mating (as indicated by clasping) just 14 days after they had hatched. The last four pairs mated in 25 days. The average time required to reach mating maturity after hatching was 16 days. The minimum period observed in earlier experiments at Scripps Institution was ten days. The period of clasping varied from a few hours up to one or more days, but there was no evidence that the actual transfer of the spermatophore to the female is delayed until she molts to the last or sixth copepodid stage. Clasping was rarely observed before the female had reached the sixth copepodid stage, and on only one occasion was there evidence of molting during the clasping period. This point deserves further study. Williams (1907) found that for the harpacticoids, *Harpacticus uniremis, H. gracilis,* and *Tachidus littoralis,* "every successful copulation must be prolonged until the female molts."

Length of generation

The lapse of time between the hatching of one generation and the first appearance (hatching) of the next generation resulting from the above matings varied from 17 to 24 days at temperatures of 17° to 18° C. during the spring months. The maximum period observed in one case was 31 days. In 1935, two individuals required 20 days and one individual only 16 days. MacGinitie (1937) in an incidental statement records that this species completes its life cycle in ten days at Corona del Mar, California.

The time required for *Tisbe* to develop from egg to production of eggs is comparable to that reported for various species of the freshwater cyclopoid *Cyclops.* Ewers (1936), for example, found that for 12 species under observation the time varied from 8 to 50 days.

It appears that *Tisbe furcata* may complete its life cycle in about one-half the time required for *Tigriopus fulvus* which under favorable conditions in the laboratory at University College of Hull required about two months (Fraser, 1936). However Tsen-Hwang Shaw (1938) states that for this species at Pacific Grove, California, the adult stage is reached in about one month. It is probable that the Pacific Grove species is distinct from *T. fulvus,* since Monk (1941) mentions only *T. californicus* from the coast.

Number of broods produced

In order to determine the approximate number of broods produced by a single female, four of the above 87 pairs in copula were isolated in individual dishes. Several additional males were added to each dish to afford ample opportunity for additional matings, and the males were replaced from time to time with younger mature males. (Lowndes, 1933, and Fraser, 1936, infer that the presence of males stimulates egg production.) Nauplii were removed from the dishes as soon as they appeared. Records were kept of the number of egg-sacs produced by each female under these conditions. One female produced 12 broods between May 9 and June 10. Two other females each produced nine broods in the same period and one produced five broods in 20 days before dying, apparently prematurely. The first egg-sacs produced were the largest, and the last two or three produced were about half the size of the first. The egg-sacs appeared with regularity, two to five days elapsing between hatchings with three days as the average period.

Although males were kept in the presence of the females during the whole period, only one mating was observed to take place and this preceded the entire period of egg laying. In order to test further this observation in a more crowded condition as often occurs in nature, four separate cultures were set up each containing from 8 to 20 pairs of newly matured adults in copula. A total of 54 pairs were involved. All pairs in any one dish were from the same brood and therefore of the same age. At two day intervals all adults were transferred to fresh culture dishes so that their generation could be kept separate from the younger generation constantly being produced. These adults were maintained from May 12 to June 12, and during the time following the separation of the pairs originally mated, only one instance of a second clasping was observed. This instance occurred 21 days after the original mating, and it is not known if a spermatophore was transferred. The pair concerned was isolated from the rest of the culture in order to determine if the female would continue to produce eggs for a longer time than the other females as a result of this second mating. However, no additional eggs were carried by her. This is in agreement with the earlier observations where in one case a succession of seven broods was produced by a female that had been reared in culture and isolated following one mating. She lived 70 or 71 days but produced no eggs after the 53rd day. In another test 11 ovigerous females isolated from the general population produced two to five broods, but it is not known if previous broods had been produced before isolation. Nicholls (1935) has reported a case in which a female specimen of *Longipedia scotti* had produced at least nine broods during a period of isolation from contacts with males.

The question naturally arises as to whether or not the male of *Tisbe* produces a succession of spermatophores and remains fertile after the first mating. To test this, a single male was isolated from a group of newly matured virgin males. Several virgin females were added to the dish at intervals, and records were kept of the fertility of eggs subsequently produced by each female. Out of a total of 13 virgin females brought into contact with this one male, six produced fertile eggs which hatched. The other seven females produced eggs which failed to hatch. In another test one male fertilized eight females which produced fertile eggs.

Virgin females kept in isolation have produced full egg-sacs, but in no instance was there any evidence of parthenogenesis as reported by Roy (1931) for the harpacticoid *Canthocamptus bidens*. Pine (1934) has reported parthenogenetic reproduction in *Cyclops viridis*. This, however, appears to be a misinterpretation resulting from failure to note that several egg-sacs with fertile eggs may be produced following only one mating. The females with which she worked were doubtless already fertile since they were isolated in the gravid condition from the wild.

Discussion

Rather little is known regarding the kinds of predators that feed directly upon the littoral copepods. That this type of animal food constitutes an appreciable source of nourishment for littoral animals is suggested by the fact that only a moderate population of *Tisbe* has been observed in the sea despite a relatively rapid and steady rate of replenishment as suggested by the present study. Being detritus feeders with a wide range of acceptable food, it is probable that in favorable habitats *Tisbe* population density is controlled largely by predators. Among these predators are no doubt small fish capable of capturing small prey of this kind by pursuing and picking up the copepodid stages individually, and coelenterates having tentacles supplied with nematocysts and viscid surfaces that enable capture by chance contact. Various detritus feeders scooping up particles of detritus would consume together with this many *Tisbe,* especially the nauplii, that are prone to cling to particles upon which they are feeding.

From the present study it appears that an average of about 513 eggs is produced by each female in her lifetime. This is calculated from an average of 57 eggs per brood (using the averages of March and December) and a total of nine broods. For unknown reasons only about 80 per cent of the larvae hatched in the cultures survived to adult state. Thus, using the above figure for one female, 410 survive, of which only about 135 (approximately one third) are females. Considering a succession of generations each 25 days, a prodigious number of progeny is possible, for in about 100 days (fourth generation) over 1 billion 55 million individuals of both sexes would be produced. Ten males plus 5 females make up a mass of about 1 $mm.^3$. Hence in 100 days 70 liters of copepods would have been produced.

TABLE I

Potential rate of reproduction in Tisbe furcata and Calanus finmarchicus in cultures

	No. of broods or spawnings	No. of eggs per brood or spawning	Total no. of eggs in life-time of one ♀	Interval between generations	Survival to adult
Tisbe	7–12 average 9	29–93 average 57	513	15–31 days usually 19–24 days	80%
Calanus	1–3 (4?)	1–120 usually 15–70	Maximum observed 120	Minimum 41 days	?

These figures can of course have no significance other than to emphasize that the animal substance which *Tisbe* could supply is considerable and that a very large number of copepods must be consumed regularly by enemy predators in order to keep a balance between consumption and reproduction.

It is instructive to compare certain vital aspects of the life history of this important littoral species with similar aspects of *Calanus finmarchicus,* the most widely studied of planktonic-copepod species.

In view of the vast swarms of *Calanus* which sometimes occur in the sea, one might expect that studies of its rate of reproduction would reveal aspects suggesting possibilities of greater individual fecundity than occurs in *Tisbe,* a seemingly less abundant species. In no instance, however, is a greater rate of reproduction shown for *Calanus* on the basis of studies that have thus far been made in cultures.

Table I compiled mainly from Nicholls (1933), Clarke and Zinn (1937) and Raymont and Gross (1942) shows the great discrepancies that are brought out when comparing these two genera of widely different ecological habits.

The life span of *Calanus* is greater than that of *Tisbe,* but this appears to have no bearing on the fecundity since the number of spawnings is not shown to be affected thereby. Raymont and Gross found that under laboratory conditions *Calanus* was capable of spawning throughout the year, similar to our observations for *Tisbe,* but field observations by numerous investigators show that the rate of reproduction for *Calanus* in the sea varies greatly with season, there being a marked minimum in autumn and winter when the animals survive in copepodid Stage V. No similar field data are available for *Tisbe.*

The usually great preponderance of females over males in *Calanus* should enhance the reproductive rate provided this preponderance obtains also for the hatching eggs and provided further that there are always sufficient males in the population. That the latter is probably true is indicated by the study of Gibbons (1933). There is some evidence that in *Calanus,* as in *Tisbe,* one mating may suffice for continued spawning, since females have been observed to produce fertile eggs three or four weeks after isolation.

The greater ratio of males to females in *Tisbe* seems to have no logical explanation, since it is shown that one mating suffices for all the broods the female can produce, and each male produces a sufficient number of spermatophores to fertilize seven or eight females.

In considering this anomalous situation with respect to the relative reproductive rate of the two genera in cultures contrasted with their abundance in nature, the answer might be found in the greater ease with which *Tisbe* can be reared in culture. Hence, a truer picture might be obtained for that genus, but one that is difficult to check in the field. It is probable that in nature *Calanus* actually reaches reproductive maturity at a younger age and produces more eggs than have thus far been shown in culture experiments or deduced from field observations. An obvious alternative is that the survival rate is greater for *Calanus* (possibly because of greater opportunity for dispersal both vertically and laterally). The conclusion must then be that *Tisbe* is heavily preyed upon in its natural habitat.

Summary

1. *Tisbe furcata* is a littoral copepod that commonly invades salt-water systems connected with the sea. It is readily reared through all of its developmental stages. Being a scavenger, it thrives on various types of food, but thin slices of fresh seaweed and dehydrated kelp were especially acceptable.

2. Following the egg, there are six naupliar and six copepodid stages, the last of which is the adult. Each stage is separated by one molt.

3. The incubation period is from two to four days, usually about 2.5 days.

4. The total duration of the naupliar stage is three to eight days, usually about five days.

5. The first indication of sexual maturity as shown by clasping by the male occurred between the 10th and 25th days, usually about the 16th day.

6. The minimum time between generations (i.e., from egg to egg production) was 15 days, but usually between 19 to 24 days.

7. The span of life of individuals varied greatly. It was studied mainly in the females, some individuals of which lived for 40 to 50 days. The oldest specimen had a life span of 70 or 71 days, but no eggs were produced after the 53rd day.

8. The number of broods indicated by egg-sacs produced by isolated females varied from 7 to 12, with an average of about 9. Following the first egg sac, the subsequent ones appeared at intervals of two to five days, usually about three days.

9. The number of eggs in a brood varied from 29 to 93 with an average of 43 in one sampling and 72 in another.

10. Each female mated but once, and this mating sufficed for fertilization of all of the eggs to be produced. Males were capable of several matings.

11. About 80 per cent of the larvae hatched survived to adult state.

12. There is no evidence of parthenogenesis.

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